Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

OPINION ARTICLE

Halting Regime Shifts in Floristically Intact Tropical Forests Deprived of Their Frugivores

Jedediah F. Brodie[1,2] and Clare E. Aslan[3]

Abstract

Ecological restoration typically focuses on promoting vegetation recovery in degraded habitat or reintroducing endangered animals to enhance their regional or global persistence. Here, we argue that attention should also be devoted to vertebrate reintroductions in overhunted but floristically intact tropical forests in order to prevent insidious regime shifts in these systems. Growing evidence suggests that tropical forests deprived of seed-dispersing animals exhibit replacement of fleshy fruiting trees by species with abiotic seed dispersal. Left unchecked, this process could eventually render the forest uninhabitable by frugivores through reduced density and diversity of their food plants. In tropical areas where hunting can be controlled, we contend that frugivore reintroduction, regulation of wild fruit harvest by humans, and outplanting of native fruiting trees should be deployed as management tools long before the systems are in need of traditional habitat restoration.

Key words: alternative stable states, bushmeat, fruit harvest, overhunting, plant demography, population augmentation, rainforest, regime shifts, reintroduction, seed dispersal.

Introduction

The primary focus of the field of restoration ecology is "assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2002: 2). Most often this takes the form of enhancing native vegetation cover in disturbed habitats. This may be complemented by reintroductions of native animals, often threatened species and frequently with the implied goal of increasing their probability of global persistence (e.g. Pearce & Lindenmayer 1998; Chan & Laurence 2006). In some cases the two goals may be achieved together, such as where reintroduced animals assist in habitat regeneration (e.g. Gibbs et al. 2008).

We argue that a new strategy should be deliberately incorporated into the field of restoration ecology. Reintroducing or augmenting frugivore populations in tropical forests where they have been extirpated or depleted should be a high conservation priority to prevent long-term ecological regime shifts in these systems. Deprived of seed-dispersing animals for long enough, even floristically intact tropical forests may shift to alternative states that resemble the original condition in form but not function. Although the structure and diversity of the habitat may appear similar, animal-dispersed tree species in such systems are increasingly replaced by wind- and gravity-dispersed species. Because foundational species and interactions are then absent, a new perturbation will be required to force the community back into its original domain of attraction. This process resembles the ecosystem regime shifts that have been observed in many habitat types following extirpation of key predators with resulting cascading effects on herbivore and plant populations (e.g. Croll et al. 2005; Baum & Worm 2009). In the same vein, deliberate reintroduction of extirpated native predators can have cascading effects on plant communities via suppressing or altering the foraging behavior of herbivores (Terborgh & Estes 2010, and references therein).

Fruit–frugivore mutualisms are a hallmark of vertebrate food webs in tropical forests; most tropical trees are zoochorous (Howe & Smallwood 1982), and most tropical vertebrates eat fruit (Fleming et al. 1987). The recruitment of many tropical tree species depends on seed dispersal by animals (Terborgh et al. 2008; Brodie et al. 2009*b*). Loss of frugivore-mediated seed dispersal has recently been discussed as a key issue in the regeneration of disturbed forests (e.g. Garcia et al. 2010; Herrera & Garcia 2010), but frugivore reintroduction has received little attention as a tool for ecological restoration in floristically intact systems.

Loss of Frugivores

Pervasive overhunting in tropical forests around the world (Milner-Gulland & Bennett 2003) leads to increasingly "empty" forests that still retain trees but lack large vertebrates (Redford 1992). Indeed, large frugivores in many regions are now restricted to the few well-maintained protected areas

[1] Wildlife Biology Program, University of Montana, Missoula, MT 59802, U.S.A.
[2] Address correspondence to J. F. Brodie, email jedediah.brodie@gmail.com
[3] Environmental Studies Department, University of California-Santa Cruz, Santa Cruz, CA 95064, U.S.A.

doi: 10.1111/j.1526-100X.2011.00833.x

(Brodie et al. 2009*a*) or dwindling numbers of remote sites that are, for now, still inaccessible to humans (Peres & Palacios 2007).

Frugivore populations can also be disrupted by loss of fruits, either through reductions in fruit tree density (e.g. Barlow & Peres 2006) or fruit harvest by humans (Moegenburg & Levey 2003). Local-scale frugivore density is often linked to the density or diversity of their food plants (e.g. Mbora & Meikle 2004; Wich et al. 2004; Arroyo-Rodriguez et al. 2007).

Since most frugivores consume a variety of fruit species, it may be tempting to think that they would be robust to the loss of a subset of the tree species from the community. Indeed, many frugivores increase the diversity of their diet when their few preferred species are seasonally unavailable or lost from the community (e.g. Dunn et al. 2009). Yet "fallback foods" are often of lower nutritional quality than preferred foods (N'Guessan et al. 2009), e.g. allowing survival but reducing reproduction (Thompson & Wrangham 2008).

Trees Bereft of Animals

Frugivore populations are beset by a host of anthropogenic threats (Fig. 1). But even in highly hunted landscapes, some species may persist. Can animal-dispersed trees simply rely on these remaining species for seed dispersal? Evidence for such numerical or behavioral compensation among frugivores is mixed (Weins 1989; Peres & Dolman 2000; Kirika et al. 2008). Moreover, even frugivores that service the same tree may differ strongly in dispersal effectiveness (Brodie et al. 2009*b*).

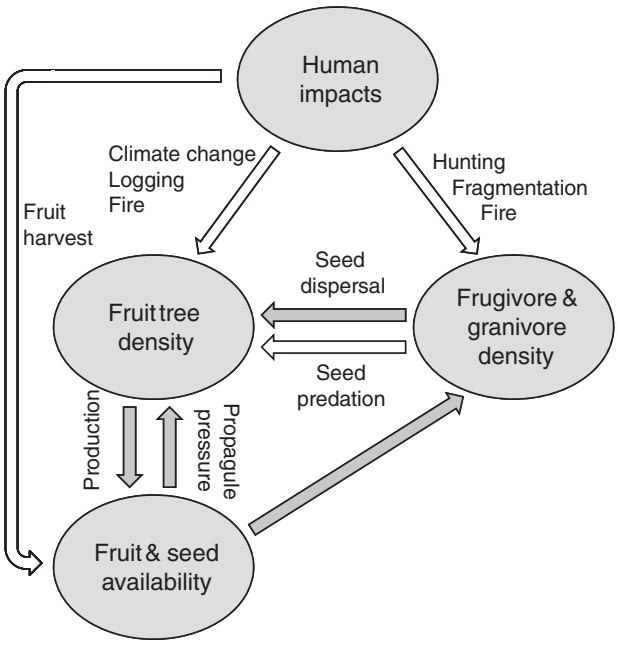

Figure 1. Schematic diagram of cascading impacts of various human activities on the density of fruiting trees and fruit- and seed-eating animals. Gray and white arrows show positive and negative impacts, respectively.

Human impacts on frugivores have particular impact on trees with large seeds. Such trees tend to depend on large-bodied frugivores for seed dispersal (Balcomb & Chapman 2003), and tree population growth rates and recruitment are therefore reduced in hunted areas (Nunez-Iturri et al. 2008; Brodie et al. 2009*a*; Vanthomme et al. 2010). In a few instances, hunting has increased tree seedling abundance by removing seed predators (Wright et al. 2000, 2007) or herbivores (Dirzo & Miranda 1991). But in most systems studied to date, forests depauperate of frugivores shift in tree species composition toward smaller-seeded or wind-dispersed species (Cordeiro & Howe 2001; Terborgh et al. 2008; Tabarelli et al. 2010; Vanthomme et al. 2010).

Ecological Restoration of Fruit–Frugivore Interactions

Over time, replacement of animal-dispersed trees in over-hunted forests by species with abiotic dispersal would render frugivore recolonization or reintroduction impossible—even if hunting could be controlled—due to the shortage of fruit for the animals to eat. We recognize that "stability" is difficult to predict in tropical forests, many of which have very long disturbance cycles, but the altered states we describe here may approximate stability because recolonization attempts by frugivores or fruiting trees could fail due to the absence of their mutualist partners. Only a sustained management perturbation (e.g. outplanting of zoochorous trees followed by frugivore reintroduction) will push the community out of its new domain of attraction and back into its original state (Fig. 2).

By evaluating current tree species composition, frugivorous animal composition, and tree recruitment, managers can determine whether the forest is already in an alternative state or may still be in its original domain of attraction (i.e. key members of frugivore-fruiting plant mutualisms are still present; Table 1). Notably, forests that have only recently lost their frugivores have not necessarily made the transition to the alternative state because fruit availability may still be high. These communities have been perturbed out of their original domain of attraction, but still have a long, gradual "settling" into their new domain of attraction as adult fruiting trees, unable to replace themselves due to recruitment failure, fade from attrition (cf. Brodie et al. 2009*a*).

When a forest appears to be in an alternative state, managers may take actions intended to shift it back into its original domain of attraction (Table 1). The strength of the perturbation necessary to return the forest to its original condition will increase over time as the community settles into its new state (Fig. 2). If neither frugivores nor fruit remain, it may be necessary to reintroduce both, along with appropriate regulation of hunting and fruit harvest by humans.

The threshold at which community regime shifts occur may be difficult or impossible to identify before it is reached (Hastings & Wysham 2010); instead, we may at present have to rely on rules of thumb for preventing state transitions. Selective logging guidelines should ensure retention of large

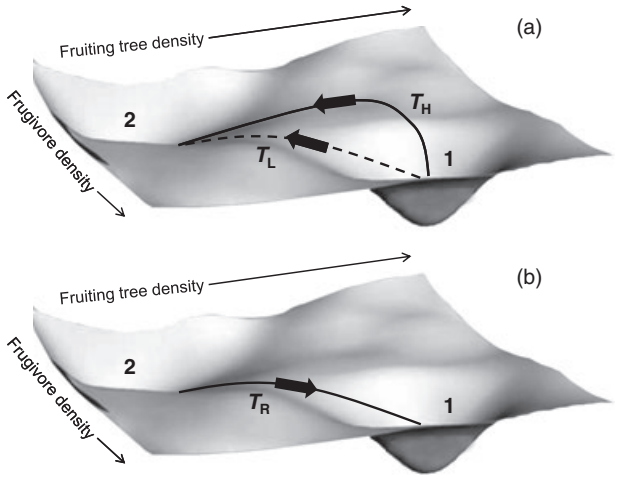

Figure 2. Transition routes between two alternative stable states in a hypothetical tropical forest. (a) If the community starts in the basin of attraction 1, with abundant fruiting trees and frugivorous animals, hunting can reduce frugivore density (solid line) until a critical threshold T_H is reached, at which point seed dispersal begins to fail, the recruitment of many zoochorous trees is compromised, and the community settles toward the basin of attraction 2, with low densities of fruiting trees and frugivores. Alternatively, selective logging can reduce fruiting tree density (dashed line), which would generate more or less concurrent reductions in frugivore density; communities will recover from light logging, but past the threshold T_L frugivore density is too low to provide effective seed dispersal. (b) Transitions from domain 2 back to state 1 will require a sustained perturbation. For example, restoration and reintroduction efforts or natural recolonization from nearby patches of intact forest could increase the density of frugivores and zoochorous trees (solid line) to the recovery threshold T_R, at which point further increases in diversity and abundance of both groups would be self-perpetuating as the community settles back toward its original configuration. Figure background adapted from Beisner et al. (2003) and used with permission from the Ecological Society of America.

fruiting trees and critical food resources such as strangler figs (Lambert 1991). Logged and deforested areas will be more prone to recover if intact forest patches remain nearby and if road access is removed following timber operations so as to limit hunting and other subsequent disturbances. Hunting across the tropics must become more sustainable; proper participation from local communities may enable this (Robinson & Bennett 2000). However, given that the relationship between frugivore density and seed dispersal may be nonlinear (McConkey & Drake 2006), forests that are "half-empty" of vertebrates may not retain effective seed dispersal (Redford & Feinsinger 2003). Therefore, it may be wise for tropical countries to consider complete hunting bans on particularly important seed-dispersing agents such as primates, hornbills, large pigeons, and fruit bats. Local community input and education will be essential for such bans to be enforceable; but where communities are involved, hunting can indeed remain (or become) sustainable (Robinson & Bennett 2000).

Although many tropical trees deprived of their seed dispersers do suffer demographically (Cordeiro & Howe 2001; Terborgh et al. 2008; Brodie et al. 2009*a*), their decline in abundance can take a long time. Yet Terborgh et al. (2008) and Cordeiro and Howe (2001) demonstrated important changes in the relative abundance of zoochorous tree saplings after only 32 and 80 years, respectively, without frugivores. The loss of the full community of frugivores and fleshy fruiting plant may result in alternative state forests that differ drastically from their previous state, are often species-depauperate, and will persist in this new form until a fresh perturbation occurs or is imposed. Strategic reintroduction of frugivores, in combination with hunting controls, fruit harvest regulation, and perhaps outplanting of native fruiting tree species, could prevent community regime shifts in biodiverse tropical forests. Deliberate maintenance of seed dispersal mutualisms in this manner may enable the ecosystem's inherent functions to contribute to its conservation by furthering the persistence of species on both sides of the seed dispersal relationship. Frugivore reintroduction therefore has the potential to be highly efficient and may save considerable restoration resources down the line.

Table 1. Examples of tools that could enable managers to assess the current state of a forest patch and, if necessary, shift it back to its original domain of attraction.

Assessment Method	*Indicators of Lost Animal–Plant Seed Dispersal Mutualisms and Possible Alternative Stable State*	*Management-Imposed Perturbations That May Shift Fragment Back Into Original Domain of Attraction*
Tree surveys	Reduced relative abundance of fleshy fruited tree seedlings and juveniles, particularly for large-seeded species	Planting of native fruiting tree species. Habitat manipulation (e.g. artificial creation of gaps in the canopy) to stimulate germination and seedling growth in shade-tolerant fruiting species
	High incidence of wind-dispersed species	
	Elevated diversity and density of exotic species	Removal of exotics
Frugivore surveys	Few large frugivorous animals	Control hunting and/or regulate fruit harvest by humans
		Efforts to stimulate natural frugivore recolonization (e.g. creation of perches, general wildlife habitat improvement)
		Artificial frugivore reintroduction

Note that methods such as these should be informed by managers' knowledge of their system; this table is intended to be general and non-comprehensive.

Successful reintroduction of vertebrate populations to achieve ecological goals is never a simple task, so restoring frugivores may be daunting for forest managers. Again, we can learn lessons from the loss and restoration of strongly interacting native predators. Successful breeding and reintroduction has been accomplished, for example, with wolves (*Canis lupus*; Parsons 1998; Carroll et al. 2003), European lynx (*Lynx lynx*; Breitenmoser 1998; Schadt et al. 2002), and black-footed ferrets (*Mustela nigripes*; Russell et al. 1994; Biggins et al. 1998). While the reintroduction of extirpated native frugivores in tropical forests has seldom been attempted, in some cases "surrogate" frugivore species have been successfully established to provide seed dispersal in lieu of the native dispersers that had been driven extinct. On Mauritian islands, for example, researchers deliberately introduced the non-native giant tortoises *Aldabrachelys gigantea* and *Astrochelys radiata* and have been tracking their performance as dispersers of large-seeded native plants (Griffiths & Harris 2010). Overall, these programs and the lessons learned from them could serve as useful guides for the successful reintroduction of native frugivores to once again fill their ecological roles in tropical forests.

Implications for Practice

- In addition to working on degraded sites, restoration ecologists should consider focusing on the protection or reintroduction of tropical frugivores in sites that currently have intact vegetation, but where loss of seed-dispersing animals could be instigating slow but dramatic shifts in tree species composition.
- Such regime shifts in forests deprived of their frugivores occur on the scale of decades; this implies that they may already be underway in the vast majority of tropical forests where vertebrate overexploitation has been rampant, but it also implies that there is still time to arrest or reverse these regime shifts.
- Controlling the hunting of frugivorous animals and the harvest of wild fruits by humans now could help maintain viable populations of seed dispersers and eliminate the need for large expenditures of resources on "traditional" ecological restoration in the future.
- Tropical forests that have already lost their frugivores and undergone shifts to abiotically dispersed tree species may require large-scale outplanting of native fleshy fruited trees, followed by frugivore reintroduction, in order to recover to their original condition.

Acknowledgments

The manuscript has been greatly improved by comments from E. Zavaleta, J. Maron, and several anonymous reviewers. The authors received postdoctoral support from the David H. Smith Conservation Research Fellowship Program, administered by the Society for Conservation Biology and the Cedar Tree Foundation.

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